PRODUCER-CONSUMER BIOMASS IN MONTANE FORESTS ON THE ARIZONA MOGOLLON PLATEAU

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ABSTRACT.— A substantially complete compilation of producer-consumer biomass was achieved for two montane forest reference stands on the Arizona Mogollon Plateau. This compilation, containing published and previously unpublished data, shows these ponderosa-pine-dominated stands to be near the lower end of the biomass range of commercial forest types. The two stands averaged approximately 75 metric tons/ha of plant biomass. Consumers made up less than 0.01 percent of the forest biomass. About 9/10 of the measured consumer biomass consisted of domestic and native ruminants.

Knowledge of biomass quantity and distribution is useful for conceptualizing biological conditions of an ecosystem, and is necessary for the study of primary and secondary production, nutrient cycling, hydrology, and fire. Information on biomass is limited for many vegetation types. Consumer data are particularly lacking in forested ecosystems where mammalian herbivores are relatively less important than in grassland ecosystems. Comparatively open forests, such as those of the southwestern ponderosa pine (*Pinus ponderosa*) ecosystem, represent an intermediate ecological position between dense humid forests and the more arid grasslands. Although large herbivores are not as obvious here as in the grasslands, their roles are significant.

Many different tree densities may occur within a forest ecosystem. Each density provides a different combination of biological components. As information is accumulated from a variety of forested conditions, more accurate judgements can be made concerning the impact of vegetation management on the amount of plant and animal life likely to be supported.

The purpose of this paper is to synthesize the current published and unpublished information on producer-consumer biomass from several representative situations within the montane forest ecosystem on the Arizona Mogollon Plateau. These values are compared to situations where the forest stand has undergone severe changes.

DESCRIPTION OF STUDY AREAS

The study areas, part of the Colorado Plateau physiographic province (Fenneman 1931), lie immediately north of the Mogollon Rim in central Arizona. The ponderosa pine ecosystem occurs at elevations between 1830 and 2590 m, although ponderosa pine is most strongly dominant between 2130 and 2380 m (Schubert 1974). It spans the altitudinal range of Merriam's Transition Zone (Merriam 1890, 1898).

Most of the information presented was obtained from the Beaver Creek watershed south of Flagstaff, Arizona (Brown et al. 1974) and from Stermer Ridge near Heber, Arizona (Ffolliott and Baker 1977). A summary of their mean characteristics follows:

	Beaver Creek	*Stermer Ridge*
Elevation	2250 m	2100 m
Precipitation	635 mm	533 mm
Temperature	7 C	9 C
Soil parent rock	basalt and volcanic cinders	Coconino sandstone
Typical soil texture	silty clay and silty clay loam	fine sandy loam
Timber basal area	26.4 m^2/ha	14.9 m^2/ha
Timber volume growth	2.8 m^3/ha/yr	2.5 m^3/ha/yr

Ponderosa pine was the major tree species on both areas. Woodland species such as Gambel oak (*Quercus gambelii*) and alligator juniper (*Juniperus deppeana*) were often

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present, and quaking aspen (*Populus tremuloides*) was occasionally found. The herbaceous layer was dominated by such graminoids as mutton bluegrass (*Poa fendleriana*), bottlebrush squirreltail (*Sitanion hystrix*), blue grama (*Bouteloua gracilis*), black dropseed (*Sporobolus interruptus*), and dryland sedge (*Carex geophila*). In some areas Arizona fescue (*Festuca arizonica*) and mountain muhly (*Muhlenbergia montana*) were prevalent. Typical forbs and half-shrubs were showy aster (*Aster commutatus*), showy goldeneye (*Viguiera multiflora*), western ragweed (*Ambrosia psilostachya*), and broom snakeweed (*Gutierrezia sarothrae*). The shrub layer was represented by Gambel oak sprouts and an occasional buckbrush ceanothus (*Ceanothus fendleri*) or New Mexico locust (*Robinia neomexicana*).

The vertebrate animal biomass was dominated by ruminants. Cattle (*Bos taurus*), elk (*Cervus canadensis*), and deer (*Odocoileus hemionus*) were the primary species. Important smaller mammals included deer mouse (*Peromyscus maniculatus*), brush mouse (*P. boylei*), Mexican woodrat (*Neotoma mexicana*), cliff chipmunk (*Eutamias dorsalis*), gray-collared chipmunk (*E. cinereicollis*), golden-mantled ground squirrel (*Spermophilus lateralis*), Mexican vole (*Microtus mexicanus*), cottontail (*Sylvilagus nuttallii*), and Abert squirrel (*Sciurus aberti*). Reptiles included eastern fence lizard (*Sceloporus undulatus*) and tree lizard (*Urosarus ornatus*). The more common birds included common flicker (*Colaptes auratus*), Steller's jay (*Cyanocitta stelleri*), white-breasted nuthatch (*Sitta carolinensis*), pygmy nuthatch (*S. pygmaea*), Grace's warbler (*Dendroica graciae*), and gray-headed junco (*Junco caniceps*). Insects and other invertebrates were excluded from this study.

Supplemental information from other ponderosa-pine-dominated montane forest stands was obtained from the Rattle Burn area southwest of Flagstaff (Campbell et al. 1977), from several wildfire burns northwest of Flagstaff (Lowe et al. 1978), and from an earlier informational synthesis (Clary 1978).

Background and Procedures

The information presented was synthesized from source data collected from the late 1950s to the late 1970s. Some of the information has not been reported previously, but much has been obtained from reports and publications from the primary reference areas and supplemental study areas. The biomass estimates are most complete on the two reference areas. Therefore, information from these will be presented as base condition for forest stands on the Mogollon Plateau. Estimates of how the biomass quantity and composition changes as tree density decreases from either cutting or fire are based on information from supplemental areas.

Assumptions for this synthesis include:

1. The primary reference areas represent typical uneven-aged cut-over ponderosa pine stands.
2. Typical forest grazing practices are followed on the cattle allotments.
3. A livestock animal-unit represents 1121 kg/ha live weight.
4. Native consumer populations have uniform distribution of sex and age classes.

Information sources used to estimate biomass are shown in Tables 1 and 2. Only aboveground living biomass near growing

TABLE 1. Sources of producer biomass estimates for Beaver Creek and Stermer Ridge.

Woody plants
- Ponderosa pine
  - —Individual stem equations from Gholz et al. (1979). (Data from Fort Valley Experimental Forest, Arizona).
  - —Stand tables from Brown et al. (1974) and Ffolliott and Baker (1977).
- Gambel oak
  - —Individual stem equations based on file data, Shrub Sciences Laboratory, Provo, Utah.
  - —Stand tables from Brown et al. (1974) and Ffolliott and Baker (1977).
- Alligator juniper
  - —Individual stem biomass based on data from Barger and Ffolliott (1972) and Miller et al. (1981), and equations from Gholz et al. (1979).
  - —Stand tables from Brown et al. (1974) and Ffolliott and Baker (1977).
- Aspen
  - —Individual stem equations from Peterson et al. (1970).
  - —Stand table from Brown et al. (1974).
- Shrubs (including Gambel oak sprouts)
  - —Field sample for current leaf and twig growth adjusted to total biomass based on Whittaker and Woodwell (1969) and Brown (1976).

Herbaceous plants
- —Data from Clary (1975) and Ffolliott and Baker (1977).

season end was calculated. Two trophic levels are presented—producers and consumers. Because no reliable carnivore information was found, no attempt was made to estimate biomass of carnivores. Also, because of a lack of insect information for the herbaceous layer, no insect biomass was estimated for modified forest conditions.

TABLE 2. Sources of consumer biomass estimates for Beaver Creek and Stermer Ridge.[1]

Domestic
- Cattle
  - —Biomass based on average animal-unit-month carrying capacities (Clary 1975) and from field sampling of fecal dropping densities.

Native
- Elk
  - —Animal-days from fecal group data of Neff (1972), Kruse (1972), Clary and Larson (1971), Ffolliott and Baker (1977), and Neff (pers. comm.).
  - —Live weight per animal from Murie (1951) and Quimby and Johnson (1951).
- Deer
  - —Animal-days from fecal group data of Neff (1972), Kruse (1972), Ffolliott and Baker (1977), and Neff (pers. comm.).
  - —Live weight per animal adjusted from McCulloch (1962).
- Tree squirrels
  - —Density estimates from David Patton (pers. comm.).
  - —Live weight per animal from Patton et al. (1976).
- Rabbits
  - —Density estimates from fecal count data of Costa et al. (1976).
  - —Live weights per animal from field sampling.
- Ground-dwelling rodents
  - —Beaver Creek biomass from Goodwin and Hungerford (1979).
  - —Stermer Ridge density estimates by field trapping with calculations according to Schnabel method (Overton and Davis 1969), and home range areas estimated from wildlife literature.
- Birds
  - —Beaver Creek breeding bird densities and live weights from Szaro (1976).
  - —Age-class distribution from Wiens and Innis (1974).
  - —Stermer Ridge bird densities determined by strip census. Live weights from Carothers et al. (1973).
- Reptiles
  - —Density estimates from strip census and calculation method of Hayne (1949).
  - —Live weight per animal from University of Arizona collection.
- Insects
  - —Direct sampling of insect biomass (dry weight) per unit weight of conifer and hardwood foliage from Ronald Young (pers. comm.).

[1]Live weight multiplied by 0.3 gives dry weight (Davis and Golley 1965).

Differences in biomass on the supplemental study areas (with and without reductions in overstory tree density) are expressed as percent change because of some differences among areas in manner of data collection.

RESULTS IN REFERENCE AREAS

Producer

Plant biomass on the two reference areas, Beaver Creek and Stermer Ridge, totaled 83,459 and 67,943 kg/ha, respectively (Table 3). Coniferous trees made up approximately 89 percent and hardwood trees approximately 11 percent of the producer biomass, and shrubs and herbaceous plants contributed only trace amounts. The conifer category consisted of 98 percent ponderosa pine and 2

TABLE 3. Producer-consumer biomass estimates.

Life form	Beaver Creek	Stermer Ridge
Plant	(kg/ha dry weight)	
Woody plants		
Trees, coniferous		
Foliage	5,638	3,733
Branches	18,272	15,015
Boles	48,125	43,785
Total	72,035	62,533
Trees, deciduous		
Foliage	432	202
Branches	2,159	1,012
Boles	8,639	4,049
Total	11,230	5,263
Shrubs		
Foliage and current twigs	18	19
Other	54	57
Total	72	76
Total	83,337	67,872
Herbaceous plants	122	71
Plant total	83,459	67,943
Animal		
Domestic		
Cattle	6.11	2.32
Native		
Elk and deer	.60	.39
Ground rodents and rabbits	.10	.03
Tree squirrels	.05	.02
Birds	.09	.04
Reptiles	.04	.02
Insects	.39	.24
Total	1.27	.74
Animal total	7.38	3.06

percent alligator juniper. The deciduous tree biomass was nearly all Gambel oak with only a trace of aspen. Woody tissues dominated. Tree boles constituted 69 percent and branches made up 24 percent of the total producer biomass. Only 7 percent of the late growing-season standing crop biomass was foliage, which is the primary food source for most of the consumer component of the forest.

These proportions vary in their comparability to other forest types. Conifer stands are often 3–5 percent foliage, 12–17 percent branches, and 78–85 percent boles (Grier et al. 1981, Whittaker and Niering 1975). Balsam fir (*Abies balsamea*) may be 23 percent foliage and only 59 percent boles (Post 1970). Hardwoods are generally 2–3 percent foliage, 18–34 percent branches, and 63–79 percent boles (Crow 1978, Post 1970, Ovington et al. 1963). Thus, the montane conifer-dominated Mogollan Plateau forests are similar to other conifer forests in their proportion of foliage, but similar to many hardwood forests in the proportion of branches and boles. A possible reason is that most southwestern ponderosa pine forests are rather open. This open characteristic may encourage the production of large branches, a trait typical of southwestern ponderosa pine (Pearson 1950).

The tree biomass in these reference stands averaged approximately 75 metric tons/ha. This value is toward the lower end of the range of 50–300 tons/ha for Rocky Mountain forests suggested by Weaver and Forcella (1977). The value appears reasonable because the ponderosa pine vegetation type normally occupies the lowest elevation and the lowest precipitation zone of the commercial forest types in the Southwest. However, in climax or near-climax ponderosa pine stands on the Santa Catalina Mountains near Tucson, Arizona, the total stand biomasses were 213–330 percent greater than the reference stands of this study (Whittaker and Niering 1975). These relatively mature climax stands had double the basal area per hectare of the Mogollon Plateau reference stands, and their average stem age of 93–150 years was probably much greater. Although the age structure of the reference stands was not determined, the large number of small stems (Brown et al. 1974, Ffolliott and Baker 1977) suggests that these stands, and indeed most cut-over southwestern ponderosa pine stands (Pearson 1950), would have a much younger average age and much less accumulation of biomass than the stands of Whittaker and Niering (1975). While the latter stands apparently represented specific situations (sampled by 0.1-ha plots), the reference stand data of this study represented the average situation across several hundred hectares of forest. It is likely, therefore, to be acceptably representative of cutover forests. In comparison to several forests in other areas, the reference stands contain biomass equivalent to 17 percent of a 180-year-old Pacific silver fir (*Abies amabilis*) stand in Oregon (Grier et al. 1981), about 73 percent of several Wisconsin hardwood forests (Crow 1978), and about 185 percent of a 26-year-old mountain maple stand (*Acer spicatum*) in New Brunswick (Post 1970).

Consumer

The producer biomass supported a comparatively small amount of consumer biomass (Fig. 1). The consumer biomass was approximately 3 to 7 kg/ha, or less than 0.01 percent of the total. Domestic herbivores, principally cattle, made up 86 percent of consumer biomass. The remainder was contributed by a variety of native species (Table 3).

Nearly three-quarters of the native vertebrate consumer biomass was contributed by the large mammalian herbivores—elk and deer. The categories of "birds" and "ground rodents and rabbits" each contributed about one-tenth of the native vertebrate biomass, although it should be noted that rabbits generally have very low populations in southwestern ponderosa pine forests (Costa et al. 1976). The remaining vertebrate biomass values were contributed by "tree squirrels" and "reptiles." The insect biomass exceeded all categories of native vertebrates except "elk and deer."

Examination of the consumer distribution suggests that a majority of the native vertebrate biomass and nearly all livestock biomass were supported by herbaceous plants, which contributed less than one-half percent

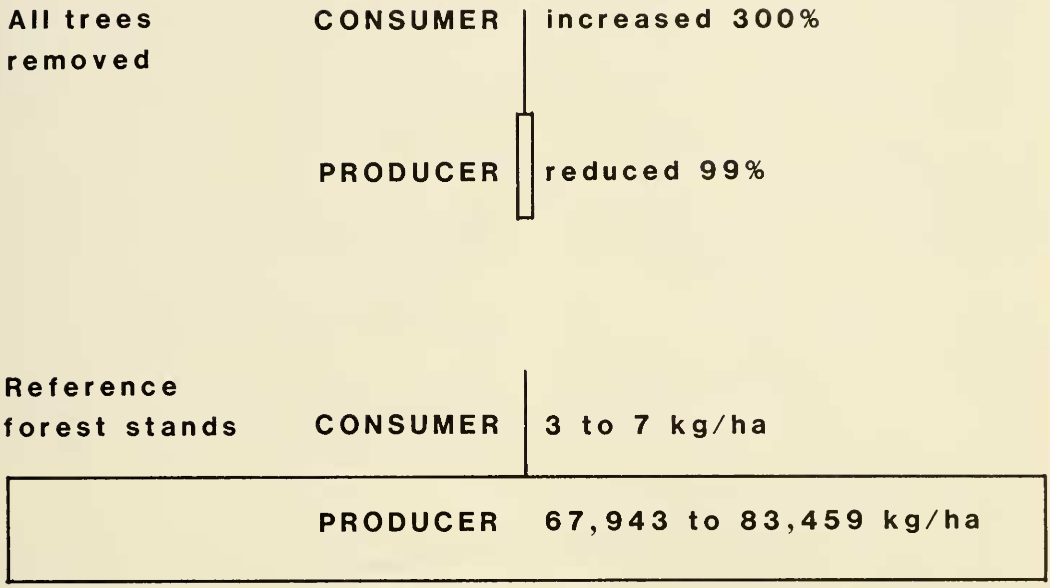

Fig. 1. Simplified biomass pyramid for reference stands, and the approximate proportional change following tree removal.

of the total biomass. Ponderosa pine trees appeared to provide the most direct food source and foraging substrate benefits to tree squirrels (Patton 1975), certain bird species (Szaro 1976), and certain insect species (Ronald Young, pers. comm.). Gambel oak foliage, which constitutes only about 6 percent of the woody plant foliage, apparently provides a substantial contribution to consumer nutrition. Oak leaves were a major component of mule deer summer diets on the Mogollon Plateau (Neff 1974), and Gambel oak foliage supported insect biomass at approximately five times the rate per unit weight of foliage as did ponderosa pine (Young, pers. comm.).

Normal activities of forest insects may be more important in energy flow and nutrient cycling than are other consumers. If consumption by insects approaches 7 percent of total forest foliage biomass (Whittaker and Woodwell 1969), insect consumption in these reference stands would approximate 350 kg/ha. This amount would greatly exceed that taken by all other consumers combined because it would exceed the total biomass of the shrub and herbage components. Insect consumption at only half this amount would still likely equal the amount taken by all other consumers.

The biomass values given represented late-growing season situations. Live biomass during midwinter would be lower. Nearly all of the herbage, all of the deciduous tree foliage, approximately one-third of the coniferous tree foliage, and a great majority of the consumer biomass would be absent then. The large herbivores, many birds, and some of the carnivores migrate to warmer winter habitats, leaving a much reduced consumer biomass.

The authors know of no other compilation of forest consumer biomass against which these reference stand estimates may be compared.

Results in Areas after Reductions in Tree Density

Several sources of information show what happened to the consumer biomass when partial reductions in the timber stand occurred (Table 4). As the forest density was reduced, tree foliage and total biomass were reduced, and the biomass of herbaceous and some shrubby plants increased. A parallel response in vertebrates occurred, with ground-feeding consumers tending to increase, and those species most directly dependent upon the trees, such as tree squirrels, tending to decrease as forest density was reduced. Some reductions in tree density occurred without reductions in bird life (Szaro 1976). If reductions in tree density result in accumulations of slash, large proportional increases can occur in small mammal populations (Goodwin and Hungerford 1979).

Total removal of trees resulted in much less foliage per hectare. Nevertheless, the increased herbaceous foliage supported a several hundred percent increase in vertebrate consumer biomass (Table 4). This increase was primarily a reflection of the difference in carrying capacity for livestock, although biomasses of many species of wildlife also increased when herbaceous plants increased. Because the productivity of herbaceous vegetation was higher, many ground-dwelling wildlife species maintained higher biomasses in the absence of trees, particularly when cover was present (Goodwin and Hungerford 1979, Campbell et al. 1977, Reynolds 1962). However, considerable variation in the densities of both small and large herbivores occurred, apparently because of cover requirements. Variations in the size of the opening, topography, presence of woody plants, and the presence of slash and other low cover will result in differences in native herbivore densities. Available information suggests variations of ± 60 percent to 80 percent will occur. Animal species shifts also occur as openings become large if little cover is present (pronghorn replace elk and deer, for example) (Clary 1978).

Tree squirrels and many birds were usually supported in higher biomasses in the forest than in the openings (Patton 1975, Szaro 1976). However, total bird biomass sometimes actually increases following tree removal when smaller tree-foraging birds are sufficiently replaced by larger ground-foraging species (Lowe et al. 1978). Different responses by birds to areas with trees removed were probably due to differing residual habitats. Little habitat variety remained after complete logging, whereas wildfire left a large number of standing dead trees that provided specialized habits for certain bird and small mammal species.

CONCLUSIONS

The ponderosa-pine-dominated reference stands on the Mogollon Plateau averaged approximately 75 metric tons/ha of plant biomass. Consumers made up less than 0.01 percent of the total forest biomass, but increased in stands where tree densities were reduced. However, even the loss of all trees resulted in a gain of only 20 to 30 kg/ha of consumer biomass.

These montane forests are near the lower end of the biomass range for commercial forest types, but we know of no forested situation for which equivalent estimates of consumer biomass are available. Therefore, no

TABLE 4. Percentage estimates of several biomass responses to reduction in forest stand densities.

	Percentages				
	Several ages of thinning[1]	Recent wildfire burn[2]	Recent wildfire burn[2]	Several ages of wildfire burn[3]	Several ages of logging[1]
Woody plants	29 decrease	44 decrease[4]	94 decrease[5]	99 decrease	100 decrease
Herbaceous plants	57 increase	128 increase	195 increase	270 increase	451 increase
Domestic animals					
Cattle	51 increase	14 increase	145 increase	—	375 increase
Native animals					
Elk and deer[6]	67 increase	125 increase	90 increase	105 increase	200 increase
Ground dwelling rodents	100 increase	109 increase	65 increase	40 increase	200 increase
Tree squirrels	50 decrease	—	—	—	100 decrease
Birds	no change	—	—	73 increase	90 decrease
Insects	—	—	—	—	—

[1]Clary 1978
[2]Campbell et al. 1977.
[3]Lowe et al. 1978.
[4]Basal area change.
[5]Commercial volume change.
[6]Biomass of these larger animals is not supported on a continuous basis in forest openings because of their movements in and out. The biomass value given is proportional to the amount of use received.

comparisons are possible for the ability of the Mogollon Plateau forests to support consumer biomass in relation to other forest types. We do know that, because most of the vertebrate consumer biomass consisted of ruminant grazers, the secondary production in this forest is easily channeled into meat supplies for people.

We feel there should be more thorough investigations of biomass components of most biological systems. This would provide an improved basis for the understanding of the basic structure and functioning of natural and modified ecosystems.

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